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**Examensarbete i ämnet biologi**

Department of Wildlife, Fish, and Environmental studies

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## Abstract

The wild boar (*Sus scrofa* L.) has expanded across Europe and Sweden in the last decades. It is a generalist species which utilizes a variety of habitats, and its presence has been shown to have both positive and negative effects for people and the landscape they are in. The abundance and increase of wild boar has previously been shown to differ between counties in Sweden, but there have been few explanations as to why.

In this study, I investigated correlations between the per capita rate of change ( $r$ ) among wild boar populations in Sweden and a variety of different habitats on the county level. I also investigated if fragmentation per se or in certain habitats could be associated with the wild boar's per capita rate of change.

My results show that fragmentation/diversity per se was not correlated with wild boar  $r$ . I found a negative correlation with the amount of deciduous trees in general, including oak, human activities (hunters/km<sup>2</sup>, traffic density and population density) and most agricultural variables (except oats). The results regarding clear cuts were inconclusive and would require further investigation. My results show a positive correlation between wild boar  $r$  and percentage of most types of coniferous and mixed forests, trees 21-60 years of age and the area of oats grown. The results agree with my results of fragmentation among similar habitats, where mean area, proximity to same habitat and others were positively correlated with  $r$ .

## Sammanfattning

Vildsvinet (*Sus scrofa* L.) har kraftigt ökat sin utbredning i Europa de senaste årtiondena. Det är en generalist som utnyttjar väldigt varierande habitat, och dess utbredning gett både positiva och negativa effekter på landskapet och för befolkningen i dessa områden. Tidigare har det visats att förekomsten och förökningen av olika vildsvinspopulationer har skiljt sig mellan olika län i Sverige, men få förklaringar till detta har getts.

I denna studie har jag undersökt korrelationer mellan den nuvarande ökningstakten per capita ( $r$ ) hos vildsvinsstammar i Sverige och ett antal habitats- och mänskliga faktorer på länsnivå. Jag har också undersökt om habitatfragmentering i sig eller av specifika habitatstyper kan vara av betydelse för att beskriva vildsvinens per capita-ökningstakt. Mina resultat visar att fragmentering i sig (oberoende av habitattyp) inte har någon stark korrelation med  $r$  i min studie.

Jag hittade negativa korrelationer mellan  $r$  och andel lövträd i länen, inklusive ek, mänskliga aktiviteter (jägartäthet, trafikdensitet och populationsdensitet) samt andel av de flesta grödor som odlas (förutom havre). Resultaten angående andel och fragmentering av kalhyggen var otydliga och skulle behöva undersökas ytterligare. Jag fann också i de flesta fall en positiv korrelation mellan ökningstakten ( $r$ ) och andelen barr- och blandskogar, träd med ålder 21-60 år och andelen havre som odlas av den totala länsarean. Dessa resultat överensstämmer i de flesta fall väl med resultaten av mina analyser om fragmenteringseffekter på habitatsnivå, där medelarea, närhet till områden av samma habitattyp m.fl. var positivt korrelerade med  $r$ .

## Introduction

For a long time, species have spread to, or invaded new habitats. In many cases this has also changed the ecological community (Geisser and Reyer 2005), and a lot of research has been conducted about invasive species (Mooney and Cleland 2001, Sakai et al. 2001, Strayer et al. 2006, to mention a few). The human population has been growing, and will continue to grow by billions over the coming 100 years (Anon 2014).

As in most of the world, the habitat in Sweden is heterogeneous, the human population is growing (Lundgren 2014), and the landscape has changed during the last 200 years (Östlund et al. 1997). Add to this that there are “invasive” species living in Sweden, i.e. the wild boar (*Sus scrofa* L.) (Anon 2010).

The wild boar exists on all continents except Antarctica (Oliver and Leus 2008), and has since the 80s spread widely across Europe, including Sweden (Geisser and Reyer 2005) (Figure 1).



Figure 1. Wild boar distribution in the world. Question marks denotes occurrence but unknown distribution, circles indicate islands where wild boar has been introduced (modified from Barrios-García and Ballari 2012).

The wild boar previously existed in Sweden, but was hunted to extinction several hundred years ago; due to escapes from enclosures a very viable population has formed in most of southern Sweden (Truvé and Lemel 2003, Anon 2010), and wild boar is now expanding its range to the north (Truvé 2004). Even though wild boar is now officially considered to be a native species by Sweden, it could be argued to be “re-invasive” as well.

The presence of wild boar has had many different effects. It has become a species for hunters, economic benefits from hunting tourism, meat (sales and the hunters’ own consumption), and the boar itself does a lot of rooting that may help increase the diversity of plants and animals (Anon 2010). However, the effects are not solely positive. In areas where the boar is not native (e.g. the Smoky Mountains of the U.S.A.) there have been reports of large ecological consequences, like increased predation on and competition with native animals, destruction of wildflower areas, damage to tree roots and woody seedlings (Mitchell et al. 2007), soil erosion etc. (Bratton 1975, Barrios-Garcia and Ballari 2012). In

Sweden the wild boar has affected agricultural crops by trampling and foraging, destroyed gardens and golf courses by rooting, caused traffic accidents and other economic loss (Herrero et al. 2006, Bueno et al. 2009, Anon 2010, Lagos et al. 2012, Schön and Ball 2013).

### **Wild boar ecology**

Wild boars are omnivorous with a preference for vegetable food with high nutritional value (Schley and Roper 2003, Barrios-Garcia and Ballari 2012). The diet is largely determined by availability, which means that there are seasonable changes in diet (Schley and Roper 2003, Massei et al. 1996). The staple food, if available is mast, like beechnut (*Fagus* sp.), acorns (*Quercus* sp.) and chestnut (*Castanea* sp.) and some consumption of animal food, like earthworms, rodents, moles, eggs and so on almost always also occurs (Schley and Roper 2003, Barrios-Garcia and Ballari. 2012). Among agricultural crops in Sweden, Wretling-Clarín and Karlsson (2010) found a preference for wheat, oats, peas and potatoes, as well as different types of grazing areas. Schley et al. (2008) found a negative selection for barley.

The wild boar utilizes an extremely wide range of habitats opportunistically (Massei and Genov 2004), and are mostly active during the night, when they are out foraging (Boitani et al. 1994). Truvé (2004) has shown that each foraging period lasts on average 7.2 hours, and that they normally move in an area of 104.4 ha (rarely ever over 400ha) in Sweden. This would represent a circle with a diameter of 1.2 km (rarely ever more than 2.3 km). This is also consistent with a Polish study in a mixed forest habitat where the average home range was 80-150 ha (Górecki et al. 2009). However, home range size can vary greatly, between 300 and 15000 ha (Massei and Genov 2004 (and references therein)).

The home range is thought to be influenced mainly by two things, food availability and density of wild boar. Increasing food availability decreases movement and home range size to reduce risk and energy spending (Massei et al. 1997). A high density of boars should in theory mean smaller home ranges and an increased activity, but if connected to food availability it might as well mean that a high density and low food availability forces the boars to increase their home range to find enough food, and the opposite if resources are high and density low (Bertolotto 2010, Massei et al. 1997).

Melis et al. (2006) found that the strongest environmental correlations with wild boar densities were the mean January temperature (i.e. winter harshness; negatively correlated) and vegetation productivity (i.e. food resources; positively correlated). These two can be connected, as Truvé (2004), Bertolotto (2010) and Keuling et al. (2008) found that snow restricts and limits wild boar food search and movement.

Within wild boar home ranges there is a habitat selection difference between day and night, where Boitani et al. (1994) found that open areas are preferably used actively during night and forest for resting during the day. In their study they also saw that some wild boar groups seemed to avoid open areas whereas others favoured them. Thurfjell et al. (2009) demonstrated that on a larger scale open areas (close to forest edges), water, and forests of different types are selected by the boar, and on a smaller scale, hedges and ditches. Most importantly, the authors also showed an avoidance of agricultural land except for the short period when crops are ripe, similar to Boitani et al's (1994) and Keluing et al's (2008) findings. Riparian and forest corridors are also often used, according to Caley (1997) and

Dexter (1998), who found that they use that habitat for thermoregulation, and Fernandez-Llario (2004) found that the selection for abundant vegetation edge habitat connected to water was connected to protecting young and increase milk production (Fraser and Phillips 1989). Choquenot and Ruscoe (2003) connected the preference for riverine woodland to pasture biomass, and found that the numerical response of pigs ( $r$ ) was lower, the longer distance between riverine woodland and pasture land.

Górecki et al. (2009) showed a preference for Scots pine and oak stands and trees older than 30 years, which partly supports the findings of Abaigar et al. (1994) who found preference for oak and mixed forests.

Turning now to spatial aspects, all habitats are composed of patches of different size, shape and type (Bowers and Matter 1997), i.e. different types of fragmentation. This is a large research topic (Skole and Tucker 1993, Herkert 1994, Andrén 1994, Kruess and Tscharntke 1994 among others), furthermore I found 23 475 hits for “habitat fragmentation” in Web of Science (2015-05-22), indicating how much ecological research focuses on this aspect of animal habitat. Depending on the structure, many variables can be quite different, e.g. the area influenced by edge. In Bowers and Matter’s (1997) review of different mammal densities as a function of patch area, they found that 20 out of 32 species’ densities did not vary with patch area, while 5 increased and 7 decreased. Turning to a consideration of wild boar in particular, Acevedo et al. (2006) found that boar abundance was highest in highly diverse forest landscapes, and Virgós (2002) found a preference for large forest fragments adjacent to other large forest fragments near mountains or riparian areas. They discuss the possibility that this is linked to the possibility of finding a larger number of key resources in a diverse habitat.

Thurfjell et al. (2015) reported that wild boar avoids high traffic levels, and most traffic accidents with boar occur at intermediate traffic levels, and mostly within the boar foraging habitat.

### *Reproduction and expansion*

The wild boar population in Sweden is expanding by 4.8 km per year (Truvé 2004), and has spread a lot since it re-established (Figure 2) (Wretling-Clarín and Karlsson 2010)

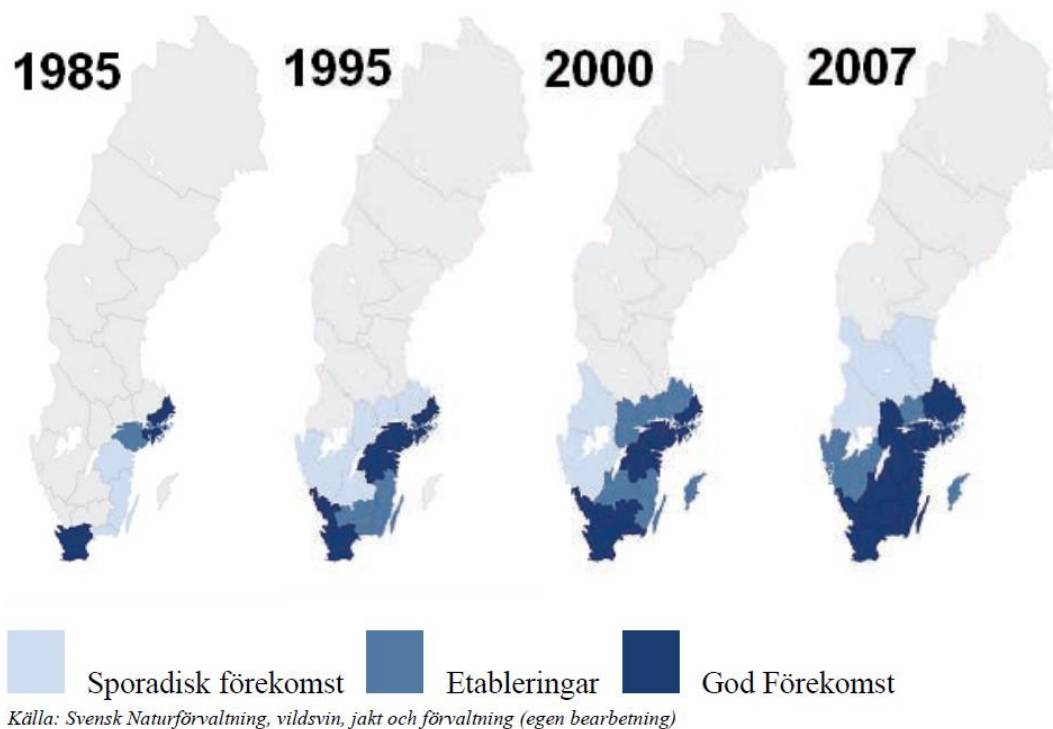


Figure 2. The geographic distribution of wild boar in Sweden 1985-2007. Sporadisk förekomst: sporadic occurrence, Etableringar: establishments, God Förekomst: abundant (modified from Wretling-Clarín and Karlsson 2010).

Turning now to the per capita rate of increase  $r$ , generally, in an expanding population the density is naturally lower at the edge of the expansion zone (Swenson et al. 1998). The density is also affected by the mortality and reproduction rate. The main cause of mortality in wild boar populations is hunting (Tolon et al. 2009). The reproduction rate is one of the key concepts to understand the success in wild boar colonization, and is also one of the main reasons why it is considered to be a problem species in Sweden. The reproduction rates reported varies greatly among different studies and landscapes; a 10% yearly increase (in Portugal) (Fonseca et al. 2011), 63% yearly increase (under good conditions in Germany and eastern Europe) (Bieber and Ruf 2005), around 40% yearly increase in the Great Smoky Mountains (Bratton, 1975), and an average litter size of 4 to 5 on the Iberian Peninsula (Fonseca et al. 2004, Bertolotto, 2010). The fecundity of the wild boar is partly affected by food availability, Bertolotto (2010) found that it affected the number of pregnant females, the size of litters and the survival probability of piglets.

### Aims

Wild boar is an intriguing species, and previous studies have shown (as seen above) a connection between boar and a variety of habitat and human factors. To determine the abundance of wild boar by field work alone is practically impossible (Acevedo et al. 2014), so there is a need to explore the wild boar-habitat relationships to be able to predict and understand current and future population trends and spread.

In this thesis I ask the following questions:

1. What is the current spread and per capita rate of change among wild boar populations in Sweden?
2. Does the per capita rate of change differ between different counties? If so:

3. Are there habitat variables that are associated with variation among counties in the wild boar per capita rate of increase ( $r$ ), and in that case, which habitat variables?
4. Is habitat diversity/fragmentation on either a county or habitat type level associated with variation in the observed wild boar per capita rate of increase among counties?

I test for an association between the habitat and the rate of wild boar increase in three ways. On the county level I look at a set of habitat variables and human disturbances, such as tree species or forest variables, crops grown in different counties, the number of hunters in various counties since hunting is the main mortality factor among boars. I will also look at a set of fragmentation variables as several studies have suggested relationships with fragmented areas or habitat diversity. On a finer scale, I will look at fragmentation and diversity variables of different habitat classes within the counties.

## Material and methods

One way of estimating the rate of increase in a population is to take measure the population at intervals and transform the numbers to natural logarithms ( $\ln$ ), where the slope of the  $\ln$  values gives the per capita rate of increase (i.e. new animals per existing animal) (Messier et al 1988, Sinclair et al 2006). Underlying environmental factors have a large influence on  $r$ , and it is therefore a good estimator of habitat suitability (Birch 1948).

There is no large-scale data on wild boar numbers in Sweden, and previous studies have shown that it is a difficult species to estimate the abundance of (Cahill et al. 2003). Therefore, indirect methods are often used, and among those hunting bag statistics are often considered the most cost effective and suitable option (Acevedo et al. 2006, Honda and Kawauchi 2011).

Studies have shown that road accident data is a good and cost-efficient way of monitoring animal population trends over time (Gehrt 2002, Baker et al. 2004, Brockie et al. 2009) and therefore I collected wild boar road accident data for years 2003 to 2014 (Nationella Viltolycksrådet 2015) and also hunting bag statistics (Kindberg, pers. comm.). Reporting road accidents with wild boar is mandatory in Sweden (Anon 2015b) unlike the voluntary reporting of hunting bags. I tested if both of these measures were correlated (which is expected if both are indexing the wild boar population) and after that decided to use the road accident data. I examine the per capita rate of increase in different counties after the wild boar are established, but I do not want to include years with just a few dispersing wild boar hit by cars. Therefore my calculations start when there had been at least 3 wild boar accidents per year for a consecutive period of at least 5 years. The road accident data was then used to estimate the population change, by doing a regression line through the natural logarithm of the road accident data (Messier et al 1988, Sinclair et al 2006).

Because of the generalist nature of the wild boar, I was not sure which habitat or human variables that could be importantly associated with wild boar  $r$ , so therefore I used my knowledge of wild boar ecology and collected a variety of data on habitats and human factors at a county level that could prove to be important to include in my analysis.

I collected data on the Swedish human population numbers from Statistics Sweden (2015a), data on the number of vehicles (cars, light trucks (<3500kg), heavy trucks (>3500kg), buses and motorcycles) registered in each county between 2003 and 2014 from Statistics Sweden, traffic analysis (2015b), the total mileage driven in each county and year was calculated



from Statistical yearbook 2011 (Statistics Sweden 2012) and the total number of hunters in each county and year (2002-2013) was taken from The Swedish Environmental Protection Agency (Bladh, pers. comm.). Regarding the habitat data, land use (maps from year 2000) comes from the Swedish Environmental Protection Agency (2014), the use of fields and agricultural crops (year 2007) comes from data at Statistics Sweden (2008) and data of forest age (2006-2010) from the National Forest Survey/SLU (2015a), as well as tree group (e.g. deciduous forests, mixed forests, coniferous forests) distribution (2015b). Tree species distribution (in million m<sup>3</sup>) and % (2009-2013) comes from the National Forest Inventory, SLU (2014). Biotope protection areas (*biotopskyddsområden*) (ravine forests, old sand forests etc.), national parks and nature reserve data comes from the Swedish Forest Agency (2015). All included and excluded habitat variables can be found in Appendix 1.

In ArcMap (ArcGIS v 10.2.1) I imported a raster dataset (resolution 25x25m) of Swedish Ground Cover Data (*Svensk Marktäckesdata*) from year 2000 (Swedish Environmental Protection Agency 2014), which I split into the different counties. The data contained 57 different classes (Appendix 2) of land cover in total (not all were found in all counties), and each surface is automatically generalized to the smallest unit for the class in question (1, 2, 5, or 25 ha). I transformed the data to 8 bit signed integer tiff files to be able to later analyze the habitat diversity and removed pixels with no data (i.e. open ocean). I did however save the coastal region class of oceans as they would potentially be a useable habitat for wild boar. Class descriptor files were created by exporting corresponding attribute tables from each county in ArcMap and then saving them as fcd (Fragstats Class Descriptor) files. To do calculations of fragmentation and habitat diversity in the map material, I imported the tiff file into Fragstats (v 4.2.1.603) (McGarigal et al 2012). Fragstats is a widely-used program (340 papers in Web of Science (2015-04-30)) which allows users to calculate a variety of fragmentation indices and metrics from map material.

There are a few input measures that need to be defined in Fragstats; edge depth, proximity distance and patch connectivity distance (i.e. different distances for Fragstats to be able to calculate indices within and between patches). According to Murcia (1995), who reviewed edge effects on abiotic factors, vegetation, birds, processes (seed dispersal, nest predation etc.) and plant species composition and richness, the distance edge effects were detected into a habitat varied between 10 and 600 meters, depending on study and what effect was studied. The median value was 42 m and the average 77.9 m (not counting values where effects were noticed to the maximum distance measured). I decided that 50 meters would be a good indicator to detect most edge effects. In order to assess a proximity index (i.e. the distance from a focal patch type within which neighboring patches are evaluated) (Gustafson and Parker 1992, McGarigal 2014) I used data from the previously mentioned study by Truvé (2004), who found that the area covered during an average activity bout for wild boar in Sweden was around 105 ha (which would equal a circle with a diameter of 1.2 km). I chose the proximity distance to be 1200 meters. For the same reasons, the connectance index (number of functional joinings between patches of the same type as percentage of maximum number of possible connections (McGarigal 2014), which is considered to be a “vital element of landscape structure” (Taylor et al 1993) was also assigned a search radius of 1200 meters.

Since Fragstats uses quite a small number of input parameters to calculate a very wide variety of indices, many of these derived indices are highly correlated and differ only slightly between their calculations (McGarigal 2014). To simplify the analysis and

interpretation of results, I reduced the number of highly correlated variables. Dormann et al.'s (2013) review and computer simulation experiment suggest 0.7 as a good rule of thumb threshold value for collinearity. Therefore I created a correlation matrix and of those variables that had a correlation of more than  $\pm 0.7$ , I chose the one that had highest correlation with most others and removed the other ones. When there were only two variables correlated, I arbitrary chose the one I thought was more likely to be ecologically relevant to wild boar (based on the literature). This was done both at the county level and at the class level (Tables 1 and 2).

Table 1. The Fragstats habitat diversity variables retained and replaced from the models at the county level due to high collinearity.

<b>County level</b>	
<b>Retained variable</b>	<b>Replaced variable(s)</b>
Patch density	Edge density, Mean patch area, Disjunct core area density, Mean core area, Mean disjunct core area, Proximity index, Percentage of like adjacencies, Contagion index, Cohesion index, Division index, Simpson's diversity index Aggregation index
Landscape Shape Index	Core area index, Patch richness density Connectivity index

Table 2. The Fragstats habitat diversity variables retained and replaced from the models at the habitat class level due to high collinearity.

<b>Class level</b>	
<b>Retained variable</b>	<b>Replaced variable(s)</b>
Patch density	Edge density, Disjunct core area density, Landscape shape index
Proximity index	Effective mesh size
Mean area	Mean core area
Core area percentage of landscape	Percentage of like adjacencies

The Fragstats variables I chose to include to test the fragmentation of the different habitat classes can be seen in Table 3.

Table 3. The Fragstats habitat class diversity variables used in the analysis of fragmentation among the different habitat classes.

<b>Variable</b>	<b>Function</b>
<b>Cohesion Index</b>	Measures physical connectedness of patches of same class. Increases as patches become more clumped and aggregated.
<b>Connectivity Index</b>	Measures connectedness of patches of same class within 1200m. 0 when no connectedness or single patch, 100 when every patch is connected.
<b>Core Area Index</b>	Measures percent of patch area that consists of core. 0 when no core area, approaching 100 when patch consists of more core area.
<b>Core Area Percentage of Landscape</b>	Measures percent of landscape comprised by core area of corresponding class. 0 when core area of focal class is rare in landscape, 100 when single patch of only core.
<b>Interspersion and Juxtaposition Index</b>	Measures evenness of distribution of patches of same class. 0 when patch types are unevenly distributed 100 when all patch types are equally adjacent to all other patch types.
<b>Mean Area</b>	Mean patch area
<b>Mean Disjunct Core Area</b>	Mean disjunct core area
<b>Patch Density</b>	Measures number of patches per area unit. Number of patches per 100 ha.
<b>Proximity Index</b>	Measures proximity of equal patch types. Search radius 1200 m. 0 when no patches of same type are within 1200 m, increases with proximity.
<b>Splitting Index</b>	Measures focal patch size and subdivision. 1 when landscape is single patch. Increases as focal patch area is reduced and subdivided

To correlate the per capita rate of increase of wild boar with the Fragstats indices of habitat diversity and fragmentation, I used the multivariate method Partial Least Squares (PLS) with the NIPALS algorithm (Cox and Gaudard 2013, Palermo et al 2009) in the JMP statistical package (v. 11.2.0, SAS Institute Inc.). It is a method used to find significantly-associated variables where there are more explanatory variables (i.e. “X” variables) than observations, and where these X variables may be highly correlated (Anon 2015a, Wold et al. 2001, Brereton 2000, de Jong and Phatak 1997). The method approximates the predictors and response (X’s and Y’s) and then fits linear models in an attempt to maximize the covariance between predictors and response variable (Anon 2015a, Eriksson et al. 1995). This method does not assume normally-distributed data.

For the data on different agricultural crops, forest types, tree age and human activity, I performed PLS analyses between boar increase and the percentage of each type of the county area (county area as in Statistics Sweden 2015c). Some tree species data were measured as million cubic meters, and were thus measured as percentage of the total group that was measured in the same way.

I removed all habitat and habitat fragmentation variables that constituted less than 1% of the total county area on average, since I consider it very unlikely that habitat types occupying only the tiniest fraction of an entire county would affect the per capita rate of increase of wild boar over that county. I next used all remaining habitat and human variables (density of humans, density of hunters, mileage driven) in the PLS to test if there

were any habitat types that were associated with the per capita rate of wild boar increase among the counties. Then I inserted all counties' habitat diversity data to test if there was an overall significance for any of the fragmentation variables against wild boar increase. Next, I tested the diversity variables by the ground cover habitat type because there may be certain habitat types in which diversity/fragmentation are of importance to wild boar. In all the above mentioned PLS runs, the data was first cross-validated, and for those that had explanatory power (minimizing number of factors >0) I continued and received a VIP ("Variable Importance in Projection") value for each variable. This is based on how important it is for modeling both X- and Y (Wold et al. 2001). I used centered and scaled data (as suggested by Cox and Gaudard 2013) for comparison and included only those variables with a VIP value above 0.8, as suggested by Wold (1995). In a PLS, coefficients are given for each variable by the model but in this study I was not interested in the size of the coefficient, only if the variable was significantly positively or negatively correlated with wild boar per capita increase.

## Results

Regarding both voluntarily-reported hunter kills and mandatory road accidents to index wild boar populations, my analysis revealed a strong correlation ( $R^2(\text{adj}) = 0.84$  ( $p = <0.0001$ )) (Figure 3) between wild boar traffic accidents and kills voluntarily reported by hunters, suggesting that both were indexing wild boar abundance.

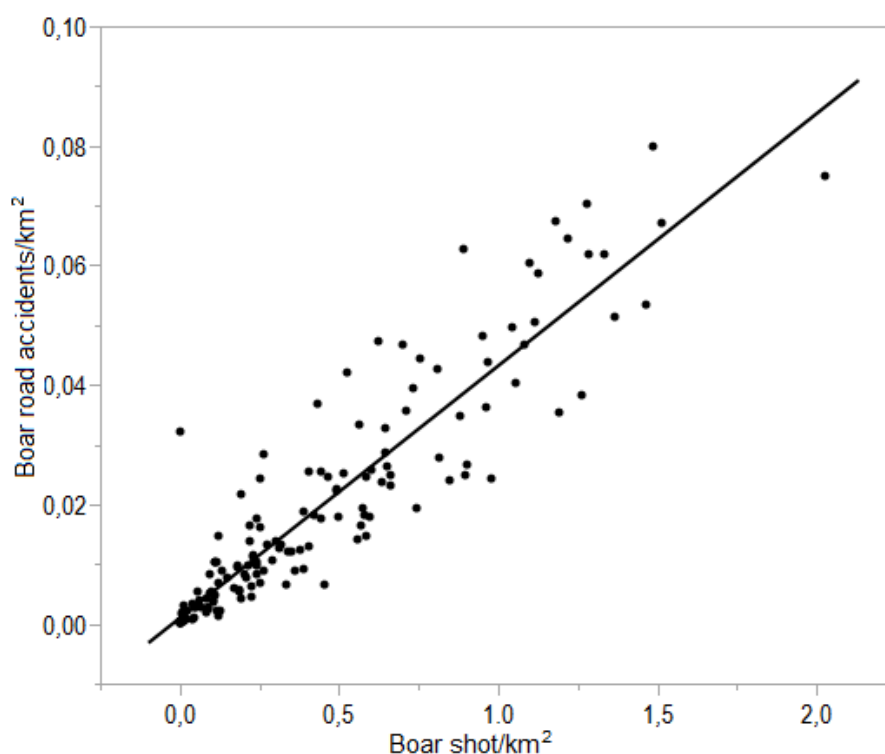


Figure 3. Correlation between boar accidents/km<sup>2</sup> and shot boar/km<sup>2</sup> in Sweden 2003-2014.  $R^2(\text{adj})$  0.84,  $p < 0.0001$ .

The current per capita rate of change ( $r$ ) was calculated by using the natural logarithm ( $\ln$ ) of the number of wild boar accidents per county in Sweden since 2003 (or when the population established if later than 2003) until present (Figure 4).

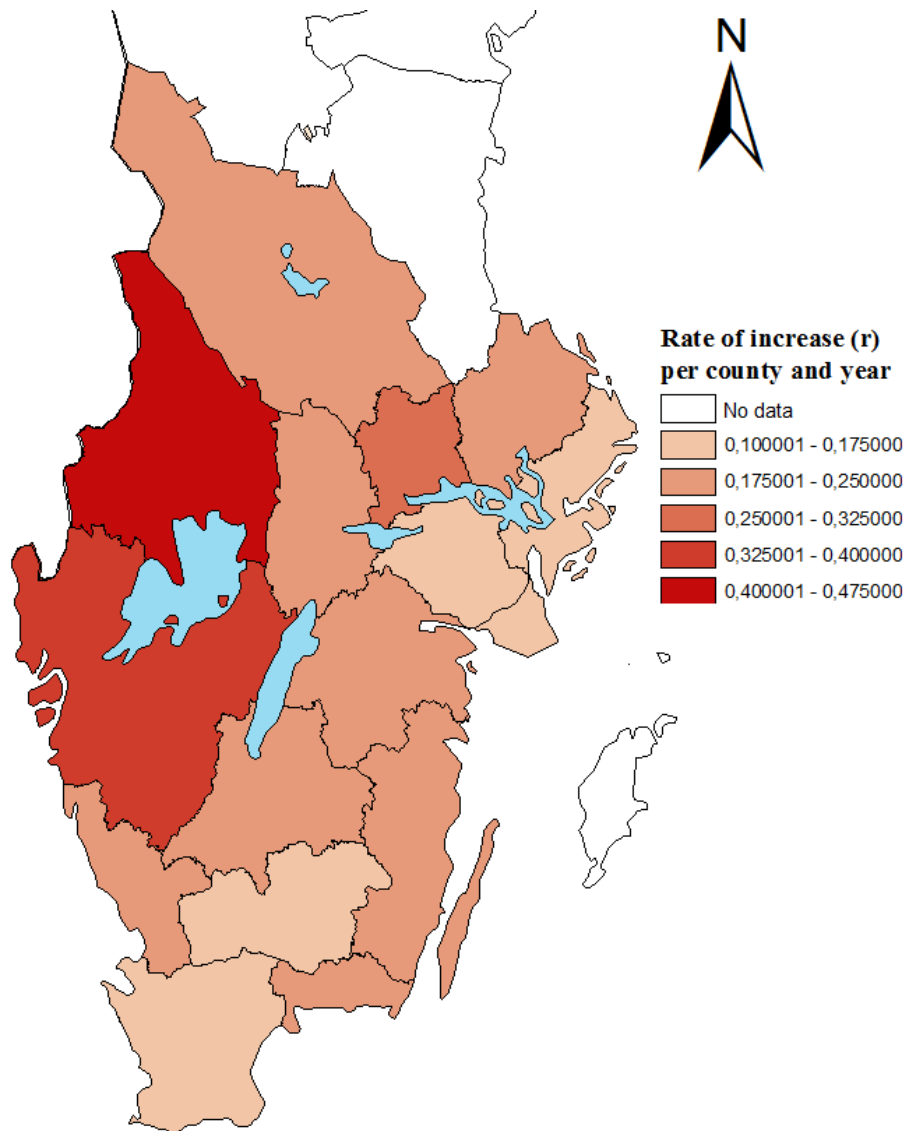
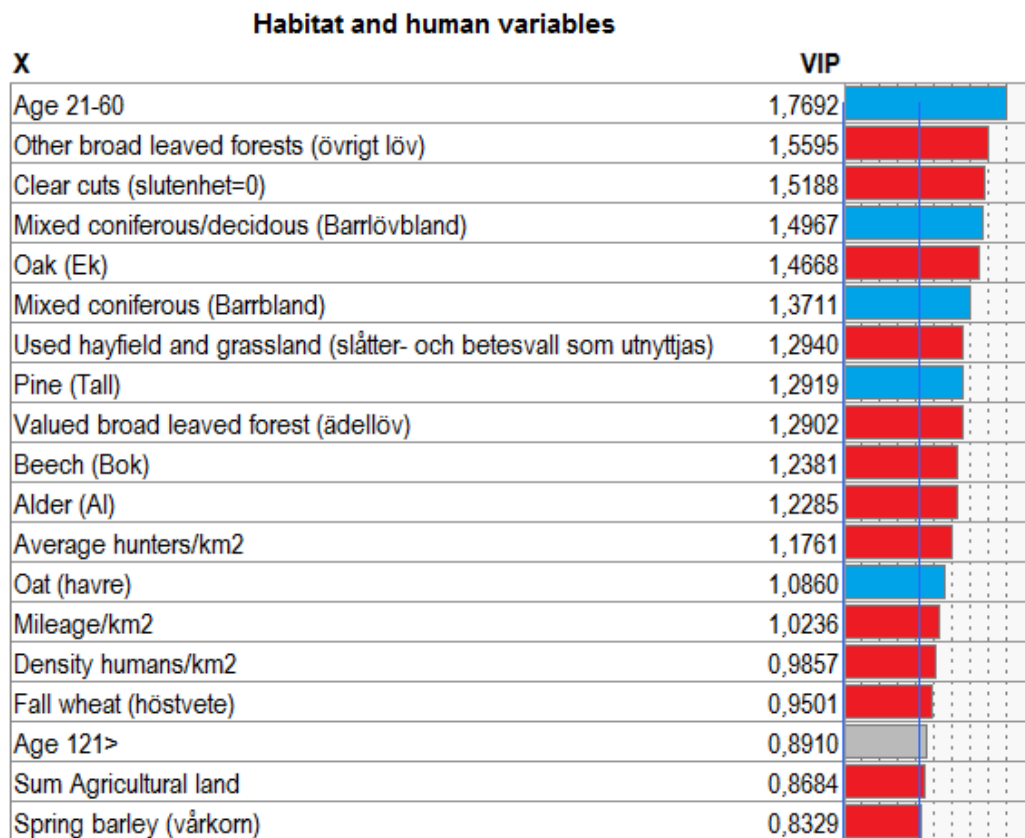


Figure 4. The per capita rate of increase ( $r$ ) among wild boar populations in counties in Sweden between 2003 (later if population established after 2003) and 2014.

There was a significant difference among per capita growth rates of wild boar among counties ( $F = 21,6140$ ,  $DF = 14$ ,  $Prob < 0.0001$ , ANOVA).

To test if the variation in per capita rate of increase of wild boar among counties was influenced by traffic intensity I did a correlation between milage driven/ $\text{km}^2$  and boar increase rate. There was no significant correlation ( $R^2(\text{adj}) = 0.04$ ,  $p = 0.23$ ). My analysis revealed the same result between the change in boar accidents between years and the change in number of registered cars per year ( $R^2(\text{adj}) = 0.001$ ,  $p = 0.27$ ).

To investigate which habitat- and human variables were associated with the wild boar per capita rate of increase, I conducted a PLS regression including all habitat variables that represented more than 1% of the area of that county as well as human density, hunter density and traffic density (Figure 5). Again, only variables with VIP value above 0.8 are included.



Cumulative X explained: 32,10%, Y: 39,55%

Figure 5. PLS regression for habitat and human variables against wild boar per capita increase. Included are the ones with Variable Importance in Projection (VIP) value > 0.8. Blue represents positive coefficient relationship with wild boar increase, red indicates negative and gray indicates no sign (coefficient <+0.01). The dark blue vertical line indicates VIP = 0.8. At the bottom is the cumulative explanatory power of the model for X (variables) and Y (boar increase).

There were no significant correlation between the wild boar per capita rate of increase and the Fragstats diversity/fragmentation data at the county level (i.e. patch/edge/shape metrics regardless of habitat type) from the Swedish Ground Cover Data (PLS regression (minimizing number of factors after cross-validation 0, minimum root mean PRESS value of 1.07143).

Looking at the habitat diversity between different habitat types I once again only used habitat types representing >1% of county area. The included habitat types and great variation in habitat composition between counties can be seen in Figure 6.

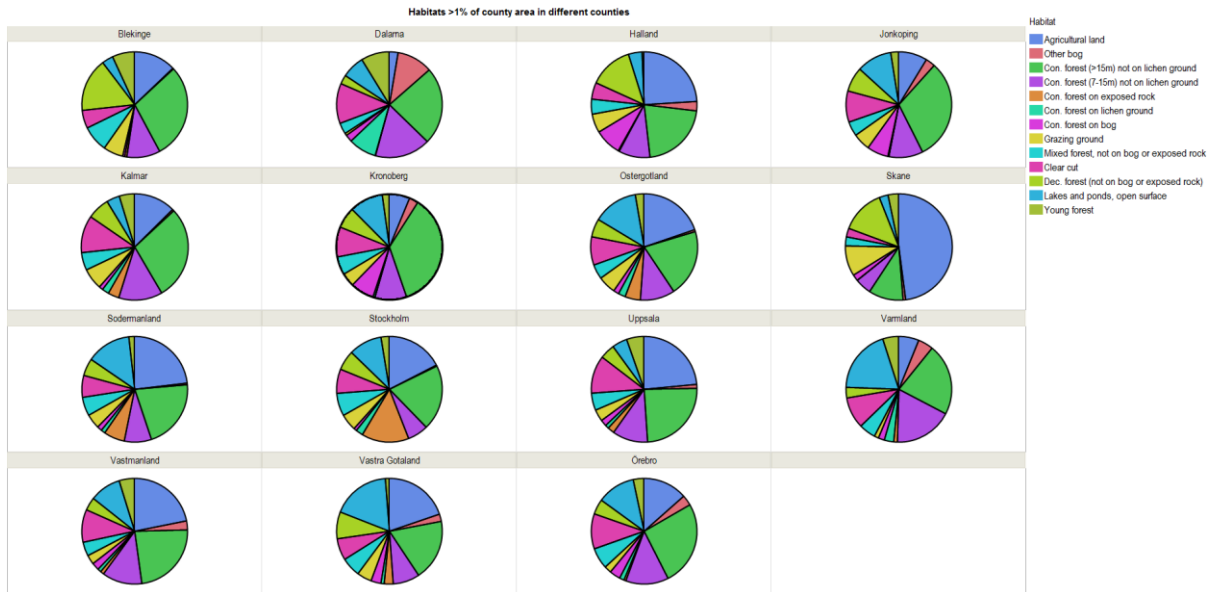


Figure 6. Pie chart of the different habitat types included in the habitat diversity/fragmentation calculations (representing on average >1% of county area). This shows the great variation in habitat composition between counties.

My analysis revealed significant PLS correlations for diversity/fragmentation variables among several habitat types and wild boar per capita increase, their correlation sign and (VIP) values are shown in Figure 7.

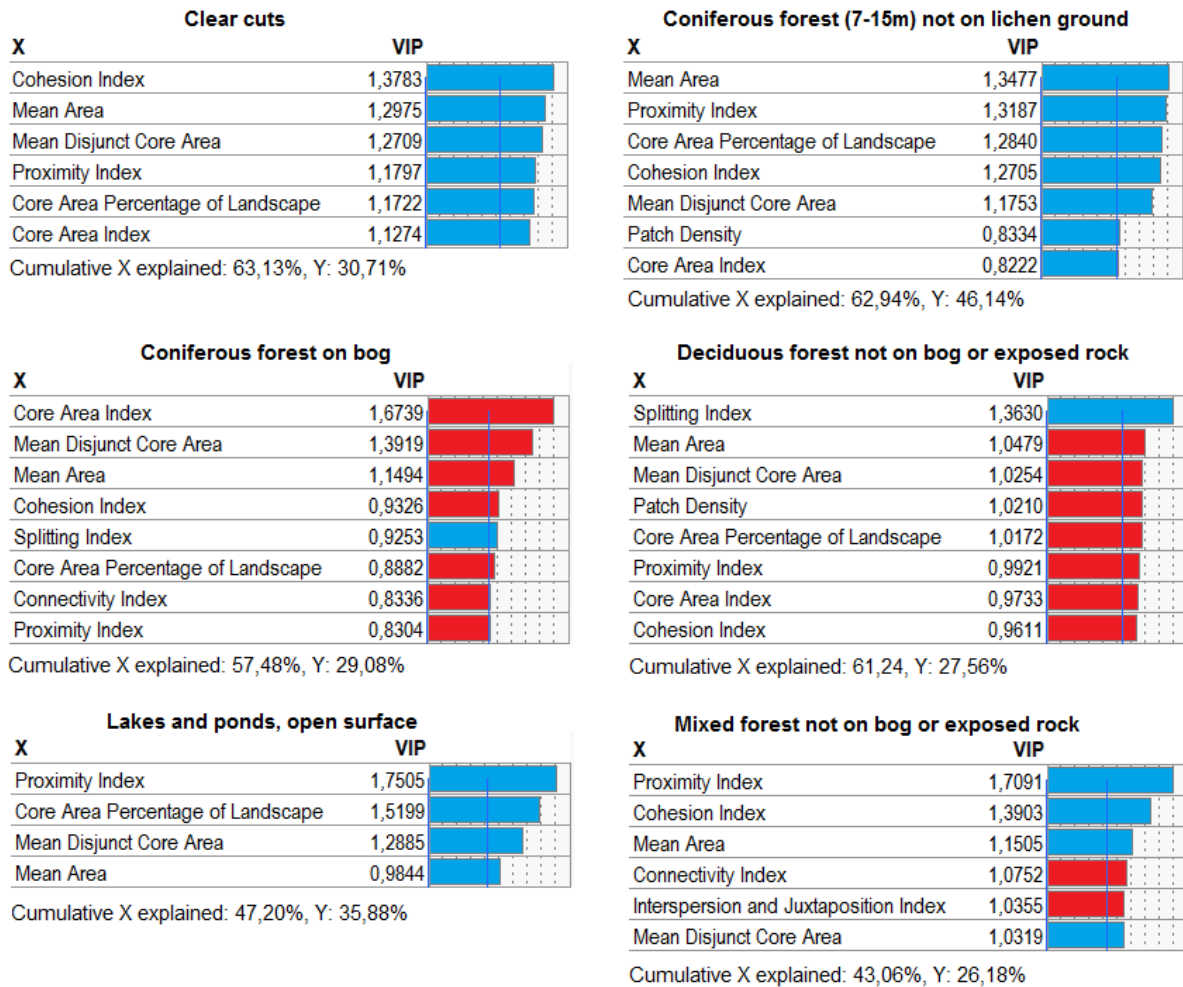


Figure 7. The six different habitat types that yielded significant correlations from the PLS, the fragmentation variables' importance in the model (Variable Importance in Projection (VIP)) and their correlation (positive: blue, negative: red). The dark blue vertical line represents VIP = 0.8. Only variables with VIP > 0.8 are included. At the bottom of each table is the cumulative explanatory power for X (variables) and Y (boar increase).

## Discussion

My analysis revealed a significant difference in mean per capita rate of change between counties, and this change over time does not seem to be connected to any increase in traffic, which means there should be other things affecting the wild boar change in Sweden.

My results show the current spread of wild boar populations in Sweden, and their per capita growth rate (Figure 4), which answers the first question in my aims (*What is the current spread and per capita rate of change among wild boar populations in Sweden?*).

I could also in this study show that  $r$  significantly differs between different counties, which answers the second question in my study (*Does the per capita rate of change differ between different counties?*), which then lead to the follow-up question: *Are there habitat variables that at a county level scale that are associated with variation among counties in the wild boar per capita rate of increase ( $r$ ), and in that case, which habitat variables?*



I found that there was a positive correlation between wild boar increase rate and the amount of trees aged 21-60, i.e. relatively young forest, pine and mixed forests, and amount of oats grown. My study found a negative correlation with deciduous trees and forests, as well as human factors and agricultural land and crops (except oats).

The last question I asked was: *Is habitat diversity/fragmentation on either a county or habitat type level associated with variation in the observed wild boar per capita rate of increase ( $r$ ) among counties?*

The answer to that from this study is both yes and no. Habitat variation/fragmentation per se was not significantly correlated with  $r$ , but among the habitat types, there were several significant correlations. Young coniferous forest (7-15 m, not growing on lichen ground cover), mixed forests (not growing on bog or exposed rock), lakes and clear cuts were generally positively correlated in terms of habitat structure; mean patch area, proximity to other patches of the same habitat. The habitat structure of deciduous forest (not growing on bog or exposed rock) and coniferous forest growing on bog were negatively correlated with wild boar  $r$ .

My results are in most instances supported by previous studies. Gehrt (2002) and Acevedo et al. (2006) have shown that road accidents and hunting bag data are good measures of species abundancy, and this study supports both those hypotheses, since both data types are highly correlated in my study. These results, plus the fact that road accidents with wild boar are mandatory to report, makes me believe that road accident data is a good index of the wild boar per capita change in different counties.

A 2009 study by Górecki et al. and Abaigar et al. (1994) found a preference of wild boar for pine forests over 30 years of age. Pregitzer and Euskirchen (2004) also showed that the net primary production is highest in boreal forests aged 31-120 years, which could be connected to Melis et al. (2006) and Bratton et al. (1982), who found that one of the most influential factors in wild boar abundance was vegetation productivity. Messier et al. (1998) also showed that pine forests had a higher cumulative understory cover than mixed and conifer forests on average.

Abaigar et al. (1994) and Thurfjell et al. (2009) also found a preference for mixed forests, which is consistent with my findings. I have not been able to find studies that either support or contradict the negative habitat diversity/fragmentation correlation between  $r$  and coniferous forest growing on bog. Speaking from my own experience I know bogs are quite open habitats they offer little shelter, and the food availability ought to be relatively low. The fact that wild boar have small hooves and relatively short legs should make it much harder to travel on bog than other forest ground. Thus it seems reasonable to believe that they would avoid bog habitat.

Agaibar et al. (1992) and Welander (2000) found a wild boar preference for deciduous forests and suggests that these are better habitat because of their mast food availability and nutrient richness compared to coniferous forests. In my study, there was a negative correlation with deciduous trees and forests, including oak. Practically all studies of wild boar suggests that oak is a very important food source (Schley and Roper (2003), Abaigar et al. (1994), Barrios-Garcia and Ballari (2012) among others). One possible explanation to this might be that my study did not take into account the wild boar's different spatial use of

habitats during day and night or during different seasons (Thurfjell et al. 2009, Boitani et al. 1994). Many studies have shown that wild boar prefer forests for shelter, and that may be what is mostly visible in my study, more than their selection of feeding habitats. It might even be that (over the course of an entire year, which was the time scale of my analysis) shelter is more important to wild boar in Sweden than food availability if food is relatively abundant and good shelter is harder to find. Another possible explanation might be that there are other factors that are not revealed in this study that allows the wild boar to increase faster in areas with more coniferous forest, like a geographical factor since there are more coniferous forest in the north, or that a more recently established population (i.e. in the northwest) is less hunted due to hunter inexperience or the desire to hunt a population before it abundant enough to make it worthwhile.

The negative correlations I found between  $r$  and human activity (here measured as population density, hunter density and traffic density) seems logical. In areas where wild boar and humans interact more, there are more conflicts and likely more attempts to reduce the boar increase. This idea is supported by the fact that my analysis revealed that traffic accident rates and hunting bags correlate very well in Sweden. It is also supported by Thurfjell et al. (2015) who showed that wild boar avoid traffic, especially high traffic levels. High traffic levels are also closely related to human density.

The positive correlation between boar increase and amount of oats grown is supported by Wretling-Clarín and Karlsson's (2010) report of cropland damages in Sweden, which showed a preference for oats by the boar. Schley et al. (2008) studied crop damages in Luxembourg and found that wild boar consumed oats less than what would be expected in relation to its abundance. There are large differences between agricultural crops in Luxembourg and Sweden, and one explanation to this could be that in Luxembourg, a lot of maize and wheat is grown, which seem to be very much selected by the wild boar. The negative correlation with share agricultural land and most agricultural crops except oats might seem strange at first, but keeping in mind that my analysis is at the level of an entire year, it fits well with studies by Acevedo et al. (2006) and Thurfjell et al. (2009) where wild boar avoided agricultural fields most parts of the year, except when crops were ripe. In the end it appears to be a trade-off between avoiding open areas (agricultural land) and utilizing the great food source oat provides.

Like Thurfjell et al. (2009) and Fernandez-Llario (2004) found, water seems to be a positively related factor to the wild boar, as my fragmentation results shows a positive correlation with lakes' and ponds' area and proximity. One thing that is harder to explain is why clear cuts in the habitat results were negatively correlated with wild boar increase; but the fragmentation results yielded all positive correlations with clear cut area, proximity and so on. I can find no logical reason for this, but it might be something for future studies to look into.

In conclusion, in Sweden, road accidents with ungulates have to be reported (so this data should be a reliable index of wild boar numbers), but the finest level of resolution this data is collected is at the county level. My analysis, which examined factors which vary among counties and tested for those factors associated with the variation in per capita rate of increase in wild boars at the county level, is thus a very logical one - no finer scale data has been collected and will not be available for any finer-scale analysis than my study. My analyses identified several factors differing among counties which were associated with the

variation in per capita growth rates, but this does combine an entire year and of course cannot address variations in the importance of daytime vs. nighttime habitats nor seasonal changes in habitat quality from the perspective of the wild boar. I found positive correlations for lake and most types of coniferous forest habitats, and negative for deciduous forests. Most of these results were also supported by the fragmentation data analysis, which showed that the fragmentation/diversity of preferred habitats also is also associated with the variation in per capita growth rates. My results on deciduous forests and clear cuts differs from some of the published literature, so could benefit from further investigation. Overall, my findings agree with many previous studies which conclude that wild boar abundance seems to be related to food and shelter availability, but that wild boar are very much more generalists than habitat specialists. This information might prove useful in further investigations among the wild boar populations in Sweden in order to predict the population increase and spread, and in the longer run take preventive measures to reduce the conflicts between wild boar and humans.

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## Appendix 1.

### Included variables that average >1% of county area and excluded variables (average <1% of county area)

<b>(Tree) Age 0-20 years</b>	Alder swamps (Alkärr)	Not specificerad agricultural land (ospecificerad åkermark)
<b>(Tree) Age 121&gt; years</b>	Bog islets (Myrholmar)	Old grazing characterized forest (Äldre betespräglad skog)
<b>(Tree) Age 21-60 years</b>	Broad-leaved dec. forests (ädellövskog)	Old natural forests (Äldre naturskogsartade skogar)
<b>(Tree) Age 61-120 years</b>	Brown beans (bruna bönor)	Old sand forests (Äldre sandskogar)
<b>Alder (Al)</b>	Burned ground (anlagda och naturliga brandfält)	Old tree land (Mark med mycket gamla träd)
<b>Aspen (Asp)</b>	Calcerous forests (Kalkmarksskogar)	Other broadleaved (Övr. lövträd)
<b>Beech (Bok)</b>	Creeks, ponds and surrounding land (Mindre vattendrag och småvatten med omgivande mark)	Other species (andra växtslag)
<b>Birch (Björk)</b>	Cultural landscapes, pastures etc (Kulturmark, hage, skogsbeta)	Other unused agricultural land (annan obrukad åkermark)
<b>Bird directive</b>	Dutch Elm (Alm)	Peas and vetch (kok- och foderärter, vicker och åkerbönor)
<b>Clear cuts (slutenhet=0)</b>	Edge zone, corridors, creeks, ravines (Kantzön, korridor, bäck, ravin)	Peas for canning (konservärter)
<b>Fall wheat (höstvete)</b>	Energy forest (energiskog)	Potato (matpotatis)
<b>Fallow (träda)</b>	European Ash (Ask)	Potato (starch) (potatis för stärkelse)
<b>Habitat directive</b>	Fall barley (höstkorn)	Ravine forests (Ravinskar)
<b>Mixed coniferous (Barrbland)</b>	Fall rape (höstraps)	Rich- and calcareous fens (Rik- och kalkkärr)
<b>Mixed coniferous/deciduous (Barrlövbland)</b>	Fall turnip rap (höstrybs)	Rye (råg)
<b>Natura2000</b>	Gardening plants (trädgårdsväxter)	Screes (Ras- eller bergbranter)
<b>Nature reserve</b>	Goat Willow (Sälg)	Seed flax (oljelin)

<b>Norway spruce (Gran)</b>	Grassland for seed yield (vall för fröskörd)	Shore- or flood forests (Strand- eller svämskogar)
<b>Oak (Ek)</b>	Green forage plants (grönfoderväxter)	Spring rape (våraps)
<b>Oat (havre)</b>	Hazel groves and hazel rich forests (Hassellundar och hasselrika skogar)	Spring turnip rape (vårrys)
<b>Other broad leaved forests (övrigt löv)</b>	Herb-rich alder groves (Örtika allundar)	Spring wheat (vårvete)
<b>Pine (Tall)</b>	Herb-rich swamp forests (Örtika sumpskogar)	Successional forests (Lövbrännor)
<b>Scots pine (Tall)</b>	Hornbeam (Avenbok)	Sugar beets (sockerbeter)
<b>Spring barley (vårkorn)</b>	Island, bog islet (Ö, myrholme)	Total Biotope protection (Summa biotopskydd)
<b>Spruce (gran)</b>	Larch (Lärk)	Total Nature conservation deals (naturvårdsavtal)
<b>Total nat. park/reserve</b>	Leaf burned-like succession ground (Lövbrännelik successionsmark)	Triticale (rågvete)
<b>Used hayfield and grassland</b>	Lime (Lime)	Wells and surrounding wetlands
<b>Valued broad leaved forest (ädellöv)</b>	Lodgepole pine (Contorta)	Wild Cherry (Fågelbär)
	Mixed seed (cereal) (blandsäd (stråsäd))	
	Mountain ash (Rönn)	
	National parks	
	Natural coniferous forests (naturskogsartad barrskog)	
	Natural decid. forests (naturskogsartad lövskog)	
	Norway maple (Lönn)	

Appendix 1. Included (bold, >1% of county area on average) and excluded (<1% of county area on average) habitat variables used in my PLS.

## Appendix 2.

Different habitat classes of the Swedish Groundcover Data		
<b>Agricultural land</b>	Air field (grass)	Industry
<b>Clear cut</b>	Airport	Lakes/ponds, overgrowing surface
<b>Coniferous forest &gt;15m not on lichen ground</b>	Areas with scarce vegetation	Landfill
<b>Coniferous forest 7-15m not on lichen ground</b>	Beaches, dunes, sand plains	Locality <200 inh.
<b>Coniferous forest on bog</b>	Burned forest	Locality >200 inh. with larger green areas
<b>Coniferous forest on exposed rock</b>	Camping site	Locality >200 inh. with smaller green areas
<b>Coniferous forest on lichen ground</b>	Coastal lagoon	Mineral extraction sites
<b>Deciduous forest not on bog or exposed rock</b>	Coniferous forest not on lichen ground	Mixed forest on bog
<b>Lakes/ponds, open surface</b>	Construction sites	Mixed forest on exposed rock
<b>Mixed forest not on bog or exposed rock</b>	Deciduous forest on bog	Natural grasslands
<b>Other bog</b>	Deciduous forest on exposed rock	Not urban park
<b>Pasture</b>	Dense city structure	Overgrowing coastal ocean
<b>Young forest</b>	Estuary	Peatery
	Exposed rock	Road and railway area
	Freshwater wetland	Salt affected marshes
	Fruit and berry farming	Schrubbery
	Gold course	Single houses
	Grass heath	Ski piste
	Gravel and sand pits	Sports facility
	Harbor	Urban green areas
	Heath (excl. grass heath)	Watercourse
	Herb meadow	Wet bog

Appendix 2. The different habitat types included (bold, >1% of county area on average) and excluded (<1% of county area on average) in my analysis, from the Swedish Ground Cover data.

## SENASTE UTGIVNA NUMMER

- 2014:14      Habitat modeling for rustic bunting (*Emberiza rustica*) territories in boreal Sweden  
Författare: Emil Larsson
- 2014:15      The Secret Role of Elephants - Mediators of habitat scale and within-habitat scale predation risk  
Författare: Urza Flezar
- 2014:16      Movement ecology of Golden eagles (*Aquila crysaetos*) and risks associated with wind farm development  
Författare: Rebecka Hedfors
- 2015:1        GIS-based modelling to predict potential habitats for black stork (*Ciconia nigra*) in Sweden  
Författare: Malin Sörhammar
- 2015:2      The repulsive shrub – Impact of an invasive shrub on habitat selection by African large herbivores  
Författare: David Rozen-Rechels
- 2015:3      Suitability analysis of a reintroduction of the great bustard (*Otis tarda*) to Sweden  
Författare: Karl Fritzson
- 2015:4      AHA in northern Sweden – A case study  
Conservation values of deciduous trees based on saproxylic insects  
Författare: Marja Fors
- 2015:5      Local stakeholders' willingness to conduct actions enhancing a local population of Grey Partridge on Gotland – an exploratory interview study  
Författare: Petra Walander
- 2015:6      Synchronizing migration with birth: An exploration of migratory tactics in female moose  
Författare: Linnéa Näsén
- 2015:7      The impact of abiotic factors on daily spawning migration of Atlantic salmon (*Salmo salar*) in two north Swedish rivers  
Författare: Anton Holmsten
- 2015:8      Restoration of white-backed woodpecker *Dendrocopos leucotos* habitats in central Sweden – Modelling future habitat suitability and biodiversity indicators  
Författare: Niklas Trogen
- 2015:9      BEYOND GENOTYPE Using SNPs for pedigree reconstruction-based population estimates and genetic characterization of two Swedish brown bear (*Ursus arctos*) populations  
Författare: Robert Spitzer
- 2015:10     Hot, hungry, or dead: how herbivores select microhabitats based on the trade-off between temperature and predation risk  
Författare: Kristina Vallance